

COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENACEAE, III. THE CARPELS *

WILLIAM C. DICKISON

INFORMATION REGARDING floral morphology and anatomy of the Dilleniaceae is surprisingly scarce. Floral studies on *Dillenia*, *Hibbertia*, and *Doliocarpus* by Wilson (1937), Ozenda (1949), and Sastri (1958) provide only incomplete data. Recently, Professor C. L. Wilson has undertaken an extensive investigation of the floral anatomy of the entire family. The first contribution toward this goal (Wilson, 1965) deals with the genus *Hibbertia*.

In the present study, no attempt was made to delve into the area of floral anatomy. Instead, concentration was focused on a comparative morphological survey of the dilleniaceous carpel.

As a result of intensive morphological studies on the woody ranalian families, the nature of the primitive carpel and its initial trends of specialization have been suggested by Bailey and Nast (1943); Bailey and Swamy (1951); Swamy and Periasamy (1964). The verification and development of these trends, however, will be obtained only by extensive comprehensive investigations of all orders and families of angiosperms (Bailey & Swamy, loc. cit.).

Since the combination of characters encountered in the Dilleniaceae has suggested a position among other presumed primitive taxa (see Dickison, 1967a), the family is thought to occupy a key position in angiosperm phylogeny. With this in mind, the present investigation was carried out with a twofold objective: (1) to attempt to uncover relationships and trends of specialization within the family, and (2) to provide additional evidence to help clarify the phylogenetic affinities of this assemblage.

MATERIALS AND METHODS

Carpels of representatives of all ten genera presently considered to compose the Dilleniaceae were examined. Material was obtained largely from the author's personal collection of preserved and dried specimens. This was augmented only when necessary by flowers derived from herbarium sheets.

The most convenient method of studying carpel vascularization was through the use of cleared specimens. Successful clearing was accomplished with 5 to 8 per cent hot NaOH (Bailey & Nast, 1943) for a period ranging from twelve hours to five days. Sclerified hairs on the

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highly pubescent carpels of *Schumacheria* and *Curatella* had to be meticulously removed prior to clearing, before details of vascularization could be observed. When phlobaphene pigments obscured the vascular traces, it was often necessary to use an overnight treatment of Stockwell's bleach (Johansen, 1940). After clearing, the carpels were washed and stained with saturated aqueous basic fuchsin.

Serial sections of floral buds were obtained by the standard paraffin methods. Dried specimens were first re-expanded in 2.5 per cent hot NaOH, after which they were washed, fixed in FAA, and treated as preserved material. Staining was accomplished with safranin or a safranin-fast green combination.

OBSERVATIONS

Dillenia. The gynoecium of *Dillenia* consists of from four to twenty carpels arranged in a whorl around a conical receptacle. The carpels are sessile, cylindrically ovate in shape and have elongate, free, characteristically abaxially recurved styles. The gynoecium is glabrous or occasionally sparsely covered with unicellular unbranched trichomes. Calcium oxalate crystals in the form of raphides or crystal sand, and enlarged secretory cells are common in the wall tissue of some species.

The stigmatic region in those species investigated was indistinct and restricted to the terminal portion of the style. Hoogland (1952) reports, however, that two species (*Dillenia serrata* and *D. celebica*) have distinct, knob-like stigmas. The ovular number varies from four to about 80. The ovules are bitegmic, anatropous or apotropous and generally borne in single or double submarginal rows (FIG. 12). In *D. parviflora* it was observed that the micropylar openings in the two integuments do not always correspond. This interesting feature was first brought to my attention by Dr. G. L. Stebbins (personal communication), although it has been reported and illustrated in *Acrotrema* (Swamy & Periasamy, 1955) and *Hibbertia* (Sastri, 1958), and has now also been observed in *Davilla* and *Curatella*.

The conduplicate carpels exhibit various syncarpous tendencies. Young carpels have their ventral margins closely appressed but retain a distinct ventral suture. At maturity, the ventral suture opens but the carpel remains closed by the adnation of the free ventral margins to the conical receptacle (FIG. 12). Carpellary fusion between the ventral margin and the torus in the lower three-fourths to one-half of the gynoecium results in a solid core of tissue and isolated locules of individual carpels. There may also occur, simultaneously, varying degrees of lateral concrescence between carpels. The extent and type of syncarpy changes with carpel age and level of examination in the gynoecium. A small ventral notch is all that is evident of conduplicate folding in the styler region of the mature carpel.

The carpels of all seven species of *Dillenia* examined were uniformly vascularized by three bundles which depart from a eustele in the receptacle

(FIG. 1). The dorsal trace extends through the style and terminates in the stigmatic region, whereas both ventrals end within the top of the ovary. Each ovule is supplied by a vein originating from the corresponding ventral trace. When there are double submarginal rows (as in *D. indica*), the original trace bifurcates to supply both ovules. In some species (e.g., *D. suffruticosa*), the ovular trace may become considerably branched within the ovule. Lateral veins depart at regular intervals from the dorsal bundle to vascularize the ovary wall.

Acrotrema. From approximately ten known species of this rare, semi-herbaceous genus, only flowers of a collection by Thwaites (US 1576875) were available for examination. The gynoecium is composed of three rather small (ca. 3 mm. in length) glabrous carpels. Basally, the open conduplicate carpels are laterally concrescent along their inner surfaces, resulting in a single internal cavity. At the level of ovular insertion, the gynoecium becomes completely apocarpous with the suture of each individual carpel closed. A slender, adaxially recurved style is terminated by an indistinct stigmatic surface.

The number of ovules in the genus ranges from two to six to ten to twenty (Hoogland, 1951). Swamy and Periasamy (1955) report that the ovules of *Acrotrema arnottianum* are typically anatropous, but following fertilization become completely amphitropous. A comparable situation occurs in *Hibbertia* (Sastri, 1958).

The vascular pattern in the single species investigated (FIGS. 2, 13) is similar to that described for *Dillenia*, with the exceptions that in *Acrotrema* the ventral bundles approximate the dorsal in length, and there is a noticeable absence of lateral carpellary wall veins.

Hibbertia. The bisexual flowers of the largest dilleniaceous genus have one, two, three, five or rarely (in *H. crenata*), ten carpels (Wilson, 1965). This genus has often attracted attention because it is thought to contain members with the least specialized floral structure in the family. In some species the gynoecium is entirely apocarpous but frequently it displays varying degrees of basal syncarpy. The carpels are differentiated into a swollen ovary which is projected distally into a narrow, elongated, often abaxially orientated style; at the tip of the style is an indistinct, or slightly enlarged, stigmatic surface. The carpels vary from glabrous to densely pubescent and may contain numerous raphides crystals (e.g., *H. exutiacies*). In addition, the presence of a single druse crystal in the ovules of certain species (e.g., *H. tetrandra* and *H. cuneiformis*) is very striking. One to 25 bitegmic, anatropous, submarginal ovules are present in each ovary. As has been noted previously, the micropylar openings in the two integuments do not always correspond.

Wilson (loc. cit.) has described two distinct types of gynoecia within the bicarpellate species. He arbitrarily designates these as "opposite" and "oblique" forms. In an "opposite" gynoecium, the carpels normally have their dorsal bundles lying directly opposite each other and the ventral

sutures remain centrally located throughout the length of the carpel. In "oblique" carpels, however, the dorsal bundles depart at an angle, with a subsequent displacement of the ventral traces and sutures to one side of the carpel. The occurrence of these two morphologically dissimilar gynoecial types is clearly observable. Wilson considers the oblique condition to be specialized and suggests it may have arisen more than once within the genus.

All specimens studied were vascularized by three traces: a dorsal and two ventrals. In material of such species as *Hibbertia scandens* (FIG. 3), the dorsal bundle supplies numerous lateral veins to the ovary wall before ending at the style apex. The vascular supply to the ovules is derived from the ventral bundles.

A well documented trend of reduction in carpellary vascularization is present within the genus. For example, in *H. tetrandra* (FIG. 4) only two lateral wall veins originate from the dorsal, and the ventral bundles are much reduced. The culmination of this specialization can be found in the greatly reduced carpel of the genus *Pachynema* (see FIG. 5).

Pachynema. Two species of this Australian genus were available for investigation. The bisexual flowers contain two glabrous carpels with only slight basal fusion. Each carpel is differentiated into an enlarged ovary and a narrow, slightly reflexed, vascularized style. A very localized, apical stigmatic surface is quite indistinct. Secretory cells are very common in the ovary wall.

Reduction in the sterile ventral borders results in the conduplicate nature of these carpels becoming obscured. The bicarpellate gynoecium is best described as opposite, although this appears to be a rather unstable character with tendencies toward obliqueness being observed. The ventral sutures are typically open at the level of ovular placentation, but closed below and above this location. Variations in the degree of closure reflect differences in carpel maturity.

The reduced nature of the gynoecium in this genus is very pronounced in the pattern of carpel vascularization (FIG. 5). One dorsal and two ventral bundles enter the base of the carpel. Four major lateral veins are derived from the dorsal bundle and supply the ovary wall. The status of the ventral traces is considerably reduced with each one serving as the vascular supply to one of the two basal ovules.

Didesmandra. The gynoecium of the single species, *Didesmandra aspera*, is bicarpellate with only slight basal connation present. The carpels are very characteristically differentiated into a large, swollen, glabrous ovary and an elongate (15–20 mm.), filiform style. A stigmatic region is restricted to the style apex. Numerous enlarged secretory cells are scattered throughout the ovary wall.

The two conduplicate carpels are oblique in their orientation (FIG. 14). Even though the oblique condition is clear, it is not as pronounced as in some *hibbertias*. The conduplicate nature of the carpels is somewhat

obscured by the reduction and fusion of the ventral margins rendering the gynoecium permanently closed along its entire length.

The vascular system (FIG. 7) at the base of each carpel is eustelic. A dorsal bundle departs initially from the stele, closely followed by a pair of ventral traces. Following the departure of the dorsal and ventral carpel bundles, the stele contracts to a pithless condition and continues distally to vascularize the single, comparatively large, basal ovule. The ovular trace terminates in a series of short branches. The ovary wall is supplied by lateral veins from both dorsal and ventral bundles.

Schumacheria. All observations on this endemic Ceylonese genus were made from *S. castaneifolia*. Although the flowers are often described as possessing three carpels, bicarpellate flowers are quite common. In either case, the gynoecium is densely covered with sclerified hairs. The presence of calcium oxalate crystals in the form of either raphides or crystal sand, in addition to large secretory cells, is also characteristic for this species. The ovary, containing a single basal ovule (FIG. 16), projects distally into an elongate, abaxially recurved style which narrows at its tip to form a terminal stigma.

In bicarpellate gynoecia, the carpels are distinctly oblique in orientation. In such cases, syncarpy occurs between carpels throughout the length of the ovary by fusion of only one of their ventral borders. Also, one carpel of the gynoecium may open at maturity while the other remains closed.

In tricarpellate flowers, one carpel was found to develop at a higher level than the other two which are initially somewhat oblique. As the third carpel develops, the "obliqueness" evident basally is lost. This observation suggests that in *Schumacheria* the third carpel is in the process of being lost and the oblique condition is a result of this process. A developmental study of the flower of *Schumacheria* would perhaps aid in clarifying the origins of the oblique gynoecium.

The vascularization of *Schumacheria* carpels is quite complex but resembles *Didesmandra* in that following the departure of the dorsal and ventral carpel traces, the stele becomes pithless and forms a thick, stout ovular trace which "fans out" in the ovule into numerous small veinlets (FIG. 6). Three traces leave the stele at approximately the same level. These bundles branch and bifurcate almost immediately, however, so the carpel, for all practical purposes, is vascularized by more than three major traces. The two ventral traces do not contribute to the vascularization of the ovule. The ventrals extend to the summit of the style with the dorsal trace. Numerous lateral veins anastomose throughout the ovary wall.

The suggested close relationship of *Schumacheria* and *Didesmandra* (Hoogland, 1951) is supported by carpel morphology, pollen morphology, and wood anatomy.

Tetracera. This genus is particularly noteworthy in possessing both unisexual and bisexual flowers in an otherwise entirely bisexual family. It is interesting in this regard that Hoogland (1953) refers to the flowers

of the Indo-Malayan tetraceras as bisexual, whereas Hunter (1966) calls the flowers of the Panamanian forms unisexual. The small number of African specimens I examined possessed bisexual flowers; thus, unisexuality appears to be confined to the New World. However, additional collections will have to be studied to support such a basic distinction.

The apocarpous gynoecium is composed of one to five pyriform carpels. The carpels vary from glabrous to densely pubescent, and possess from one to twenty anatropous, bitegumented ovules arranged in two to six submarginal rows. An erect, occasionally abaxially directed, style is terminated with an undifferentiated or slightly peltate stigmatic surface. Calcium oxalate crystals in the form of raphides or crystal sand and large secretory cells are quite common in the wall tissue of some species (e.g., *Tetracera indica*).

The conduplicate nature of the carpels is apparent in both the ovary and the solid style where a persistent ventral fold remains. Characteristically, the carpels are completely closed and fused basally. Progressing distally, the ventral suture becomes histologically more pronounced with the ventral region becoming open in some species.

Carpel vascularization is as follows (FIG. 8): following the departure of sepal, petal, and stamen traces, the vascular system in the torus forms large, isolated bundles corresponding in number to the carpels. Thus, each carpel is supplied by a single, large toral trace. Upon entering the carpel base, the dorsal bundle departs first, closely followed just below the initiation of the locule by the bifurcation of the remaining toral trace into two ventral bundles. Many carpels observed had accessory carpel bundles originating from the toral bundle. These accessory veins are usually quite reduced and either end blindly or connect with other lateral wall veins. The occurrence of numerous, highly anastomosing, lateral wall veinlets between the ventral and dorsal bundles is well developed in the genus. The ovules are supplied by veins branching from the ventral traces.

Curatella. The flowers of the monotypic *Curatella americana* are normally bicarpellate, although Hunter (1966) reports that the number of carpels may rarely be one to five. The gynoecium is very densely pubescent. Syncarpy occurs between carpels by complete fusion of the adaxial ovary surfaces. The erect styles are typically free and terminated by a peltate stigmatic surface. Raphides crystals and large secretory cells are present throughout the gynoecium.

In addition to fusion between carpels, the ventral sutures of both carpels are also closed basally (FIG. 15). The ventral suture becomes more distinct at the level of placentation and may even become completely open. In the solid style a notch remains in the ventral region. The orientation of the bicarpellate gynoecium is strictly opposite.

As seen in FIG. 10, the carpel of *Curatella* is vascularized by five major bundles: a dorsal, two ventrals, and two large accessory traces. Occasionally, additional smaller supernumerary traces are distinguishable so that seven carpel traces are present. Each carpel trace arises independently

in the toral stele; however, in some gynoecia the ventrals were observed to diverge from a common sympodium. At the base of the carpel, complex anastomosing and branching occurs in the stelar system before the major carpel traces emerge. A similar situation has been reported in the Winteraceae (Nast, 1944; Tucker & Gifford, 1964). The dorsal bundle, which bifurcates at the base of the style, and the two ventrals terminate just below the stigma. The accessory bundles usually connect with other lateral wall traces departing from the dorsal. Each ventral trace supplies the vascularization to one of the two, bitegmented, basal ovules. The micropylar openings in the two integuments do not always correspond.

Davilla. This genus is uniformly characterized by monocarpellate flowers. The glabrous gynoecium is distinguished by a slightly clavate style and a flattened, peltate, stigmatic surface. Two basal, bitegmic ovules are present in each carpel, along with the rather frequent occurrence of raphides crystals. The micropylar openings in the two integuments do not always coincide.

In the Dilleniaceae, *Davilla* appears to be unique in that the ventral carpel margins are involute and not conduplicately folded. At the carpel base, the ventral region begins to open along the outer ventral surface in what would be considered a conduplicate manner. Slightly higher, however, the ventral margins become distinctly involute (FIG. 11 b), with the outer carpel surfaces being brought inside. At this level the carpel may either be closed or open. Above the point of placentation the involuted margin begins to fuse internally and eventually all evidences of the ventral suture and folding are lost (FIG. 11 c).

The vascularization of *Davilla aspera* is rather simple (FIG. 11 a) when compared to other New World genera. Three carpel traces are present at the base of the locule. The dorsal bundle extends unbranched along the length of the style, except for the departure of two lateral wall veins. Both ventrals are reduced but give rise to the vascular supply to the ovules.

Doliocarpus. With the exception of the bicarpellate *D. coriaceus*, this genus is also unicarpellate (Hunter, 1966, reports the Panamanian species may rarely possess two carpels). All species have carpels with well-differentiated ovaries and extended styles terminated by peltate stigmatic surfaces of varying size. The gynoecium is either glabrous or densely pubescent (e.g., *D. major*). Similar to many other Dilleniaceae, the carpel wall frequently contains large secretory cells. *Doliocarpus dentatus* (FIG. 9) is readily distinguished from other species by the presence of raphides crystals, which were often so numerous they obscured details of vascularization in cleared carpels.

The carpels of *Doliocarpus* are conduplicate although the ventral borders may be considerably reduced. Slight variations were observed in the degree of carpel closure. The ventral margins of *D. dentatus* and *D. guianensis* are closed basally, but at the level of locule formation begin to open internally until they become completely distinct at the level of ovular

insertion. Above the level of placentation, the carpel begins to close centripetally. *Doliocarpus major*, by contrast, remains open along the entire ovary length.

Doliocarpus coriaceus shows complete adnation between the two opposite carpels. At the level of ovular placentation, the ventral suture of each carpel opens, creating a continuous internal cavity within the gynoecium. Immediately above this point, the ventral region fuses solidly leaving no evidence of sutural structure. Separation of the style is initiated by an internal cleft which proceeds outward.

Each carpel of *Doliocarpus coriaceus* is supplied by three major bundles, a dorsal and two ventrals. The dorsal trace is well pronounced and vascularizes the style. The weaker ventrals terminate within the ovary after initiating traces to the two basal ovules. Small lateral wall veins occasionally originate from and anastomose between the ventral and dorsal bundles, as well as from the toral region.

All the monocarpellate species examined were vascularized by more than three major traces departing from the stele. Generally a distinct dorsal bundle is recognizable, which, upon entering the style, undergoes a series of bifurcations resulting in a rich vascularization of the style. Although ventral traces can often be discerned, they are not at all pronounced or distinguished from the other four to six accessory bundles. The pair of ovules is supplied by veins originating directly from the receptacle. Numerous lateral wall veins are present throughout the ovary. The complex basal branching and anastomosing observed in *Curatella* is also present in *Doliocarpus*.

DISCUSSION

Among the various species of Dilleniaceae examined, the following primitive gynoecial features were observed: (1) complete or nearly complete apocarpy; (2) visible conduplicate folding; (3) open ventral sutures; and (4) large numbers of ovules. It is clear, nevertheless, that no extant dilleniaceous carpel is closely comparable to the primitive ranalian megasporophyll.

On the other hand, the Dilleniaceae are more readily characterized by a larger number of moderately to highly advanced phylogenetic specializations which parallel those that occur in angiosperms as a whole: (1) reduction in number of carpels to one; (2) differentiation and elongation of a narrow, vascularized style; (3) formation of a restricted, terminal, often peltate stigmatic surface; (4) reduction in number of ovules to two or one; (5) varying degrees of basal adnation and/or lateral concrescence; (6) complete fusion of the ventral suture; (7) reduction or amplification of the basic three-veined carpel vascularization; and (8) tendency toward involute closure. The occurrence of the oblique gynoecium in many bicarpellate Old World species is an intriguing feature of possible phylogenetic significance.

The least specialized carpels in the family are found among the apo-

carpous species of *Hibbertia*. When considered *as a whole*, the subfamily Dillenioidae is less specialized in carpel morphology than the Tetraceroideae. This information may be correlated with that obtained from other lines of evidence, e.g., wood anatomy. The fact that direct correlations do not always hold true can be demonstrated in *Didesmandra* and *Schumacheria*, which have very primitive wood but rather specialized gynoecia, and *Tetracera*, with more advanced wood but comparatively primitive carpels. Most frequently, dilleniaceous species have various combinations of advanced and primitive characters present simultaneously. For this reason, no one subfamily or genus retains exclusively primitive or advanced features. The opinion of Hoogland (1951) that the gynoecium of *Dillenia* is the most advanced in the family is not substantiated.

According to the classical concept, the primitive carpel is a three-trace organ (Eames, 1931). The primitive nature of the three-trace condition was generally accepted in light of studies on the woody Ranales (e.g., Bailey & Swamy, 1951). From the three-trace condition, a multitrace carpel would be derived by amplification, whereas a two-trace organ would result from loss of one of the ventrals.

With the discovery of multitrace carpels in some otherwise primitive families — Degeneriaceae, Lauraceae, Winteraceae, Myristicaceae, and Annonaceae among others, the primitive nature of the three-trace carpel was questioned. Some authors, e.g., Swamy (1949), suggested that the presence of additional bundles in the monocarpellate gynoecia of *Degeneria* was indicative of a multicarpellate ancestry with the extra bundles being considered remnants of missing carpels. In reviewing the vascularization in ranalian carpels, Sastri (1959) has specifically warned against the assumption that the three-trace carpel is primitive for all angiosperms. Tucker and Gifford (1966b) are of the opinion that the three-trace concept is not essential to an understanding of carpel vascularization, and point to Sterling's (1953) conclusion that the basic pattern in the Rosaceae is five-trace.

When the vascular pattern in the Dilleniaceae is correlated with other indices of advancement such as closure, ovule number, degree of syncarpy, etc., there is little question that the three-trace condition is primitive. Specializations in vascularization have subsequently occurred toward reduction (particularly in the ventral bundles) and amplification. It appears, accordingly, that there exists a fundamental distinction in carpel vascularization between the Dilleniaceae and the Rosaceae, a family often derived through, or allied to, the dillenias.

In many species of Dilleniaceae with reduced carpel numbers, weak supernumerary traces occur which could be interpreted as remnants of a multicarpellate ancestry. However, I believe the well developed accessory bundles in the monocarpellate species of *Doliocarpus* and the bicarpellate *Curatella* are the result of phylogenetic amplification. It is entirely possible that both processes have occurred simultaneously. It should be emphasized in this connection that not all solitary dilleniaceous carpels are multitrace, a tendency noted by Tucker and Gifford (1966a). In

contrast, the unicarpellate hibbertias have three prominent traces (Wilson, 1965), whereas the New World genus *Davilla* retains the three-trace condition in a considerably reduced form.

My conclusions (Dickison, 1967a & b), based on wood anatomy and pollen morphology, that previous magnoliaceous ranalian affinities ascribed to the Dilleniaceae are not well founded also gain support from the vascular anatomy of the carpels. In some Magnoliaceae and Annonaceae, the ovules are vascularized by traces from the dorsal bundle (Canright, 1960; Periasamy & Swamy, 1956). Although there is no uniform method of ovular vascularization in the Dilleniaceae, ovular traces never originate from the dorsal bundles. The cortical system characteristic of many Ranales is also lacking in the dillenias. Likewise, the compound gynoecea and axile placentation of the Theaceae show little similarity to the Dilleniaceae.

A more comparable situation is found in *Paeonia*. The gynoeceum of *Paeonia* is apocarpous with each carpel vascularized by three principal bundles, a dorsal and two ventrals, accompanied by a variable number of smaller secondary veins. Each of the two ventral traces bifurcates at the base of the style resulting in a richly supplied stigma. It is particularly noteworthy that Brouland (1935) diagrammed a bicarpellate gynoeceum of *P. delavayi* as being oblique. Since this species is more commonly tri-carpellate, it again indicates that the oblique condition probably results from reduction within the gynoeceum. Also, the occurrence of the oblique gynoeceum in *Paeonia* suggests that this character might have phylogenetic significance in the Dilleniaceae and allies.

Unfortunately, the scanty, or nonexistent information on the floral morphology and anatomy of many families putatively related to the Dilleniaceae prevents a critical comparison.

MATERIAL EXAMINED¹

Acrotrema sp. CEYLON: *Thwaites* CP 3899 (US 1576875).

Curatella americana L. BRAZIL: *Irwin* 5470 (NY).

Davilla aspera (Aubl.) Benoist. BRAZIL: *N. T. Silva* 16.

Davilla sp. BRAZIL: *Irwin* 5570 (NY).

Didesmandra aspera Stapf. SARAWAK: *Burt & Woods* B.2540 (E); SAR 18297.

Doliocarpus coriaceus (Mart. & Zucc.) Gilg. COLOMBIA: *Haught* 1655 (US).

Doliocarpus dentatus (Aubl.) Standl. BRIT. HONDURAS: *Gentle* 1418 (MO); BOLIVIA: *Krukoff* 10407 (UC).

Doliocarpus guianensis (Aubl.) Gilg. COSTA RICA: *Skutch* 3980 (US).

¹ Material studied was obtained from the State Herbarium of South Australia, Adelaide (AD); The Forest Herbarium, Bangkok (BFK); Botanic Museum and Herbarium, Brisbane (BRI); Commonwealth Scientific and Industrial Organization, Canberra (CANB); Royal Botanic Garden, Edinburgh (E); Royal Botanic Gardens, Kew (K); Missouri Botanical Garden, St. Louis (MO); Animal Industry Branch, Northern Territory Administration, Alice Springs (NT); New York Botanical Garden (NY); Sarawak Museum, Kuching (SAR); Botanic Gardens, Singapore (SING); University of California, Berkeley (UC); and the United States National Herbarium, Washington (US).

- Doliocarpus major* Gmel. PANAMA: *Stern et al.* 223 (US).
Dillenia aurea Sm. THAILAND: BKF *s.n.*
Dillenia indica L. AUSTRALIA: Cult. BRI *s.n.*
Dillenia ovata Wall. ex Hook. f. & Thoms. SINGAPORE: Cult. SING *s.n.*
Dillenia papuana Martelli. NEW GUINEA: *Darbyshire & Hoogland* 8039 (CANB).
Dillenia parviflora Griff. THAILAND: BKF *s.n.*
Dillenia philippinensis Rolfe. PHILIPPINES: *J. V. Pancho* *s.n.*
Dillenia suffruticosa (Griff.) Martelli. SINGAPORE: Cult. SING *s.n.*
Hibbertia cuneiformis (Labill.) Gilg. Cult. K *s.n.*
Hibbertia dentata R.Br. Cult. K *s.n.*
Hibbertia exutiacies Wakefield. AUSTRALIA: *Eichler* 17965 (AD).
Hibbertia scandens (Willd.) Dryand. Cult. K *s.n.*
Hibbertia tetrandra (Lindl.) Gilg. Cult. E C3544.
Pachynema dilatatum Benth. AUSTRALIA. Northern Territory: NT 6129.
Pachynema junceum Benth. AUSTRALIA. Northern Territory: NT 6750.
Schumacheria castaneifolia Vahl. CEYLON: *Abeywickrama* *s.n.*
Tetracera akara (Burm. f.) Merr. BORNEO: UC 290527.
Tetracera indica (Houtt. ex Christm. & Panz.) Merr. SINGAPORE: *Keng* *s.n.*
Tetracera podotricha Gilg. ANGOLA: *Gossweiler* 9135 (US).
Tetracera scandens (L.) Merr. MALAYA: *s.n.*
Tetracera volubilis L. PANAMA: *Allen* 2039 (MO).

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DEPARTMENT OF BIOLOGY
VIRGINIA POLYTECHNIC INSTITUTE
BLACKSBURG, VIRGINIA 24061

EXPLANATION OF PLATES

PLATE I

Explanation of symbols: c., druse crystal; d.b., dorsal bundle; e.p., stigmatic surface; l.b., lateral bundle; ov.b., ovular bundle; ov.t., ovular trace; t., trichome; v.b., ventral bundle.

FIGS. 1-6. Vascularization of dilleniaceous carpels; only one of the ventral bundles and half the lateral veins are shown. 1, *Dillenia parviflora* (BKF s.n.), from Thailand. 2, *Acrotrema* sp. (US 1576875). 3, *Hibbertia scandens* (Cult. K s.n.). 4, *Hibbertia tetrandra* (Cult. E C3544). 5, *Pachynema dilatatum* (NT 6129). 6, *Schumacheria castaneifolia* (Abeywickrama s.n.), from Waga, Ceylon.

PLATE II

Explanation of symbols: a.b., accessory bundle; d.b., dorsal bundle; e.p., stigmatic surface; l.b., lateral bundle; ov., ovule; ov.b., ovular bundle; r., raphides; t., trichome; v.b., ventral bundle.

FIGS. 7-11. Vascularization of dilleniaceous carpels, continued: only one each of the ventral bundles and accessory bundles, and half the lateral veins are shown. 7, *Didesmandra aspera* (SAR 18297). 8, *Tetracera akara* (UC 290527). 9, *Doliocarpus dentatus* (Krukoff 10407), only the major lateral wall veins are illustrated. 10, *Curatella americana* (Irwin 5470). 11 a, b, c, *Davilla aspera* (N. T. Silva 16), from Belém, Brazil.

PLATE III

Explanation of symbols: d.b., dorsal bundle; ov., ovule; ov.t., ovular trace; s.t., stamen trace; v.b., ventral bundle; v.s., ventral suture.

FIGS. 12-16. Dilleniaceous carpel morphology. 12, *Dillenia philippinensis* (J. V. Pancho s.n., from Makiling, Philippines), transverse section of carpel, $\times 27$. 13, *Acrotrema* sp. (US 1576875), cleared and stained flower showing details of vascularization; one carpel has been removed, $\times 30$. 14, *Didesmandra aspera* (SAR 18297), transverse section of gynoecium showing large, solitary ovule, enlarged secretory cells, and oblique orientation, $\times 25$. 15, *Curatella americana* (Irwin 5470), transverse section of gynoecium in region of ventral sutures, showing complete fusion of the two opposite carpels, $\times 30$. 16, *Schumacheria castaneifolia* (Abeywickrama s.n., from Waga, Ceylon), longitudinal section of carpel showing solitary, basal ovule, $\times 27$.





